Stochastic lattice Lotka-Volterra predator-prey models

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Population dynamics is the study of interacting particle systems typically involving a number of different species, and their time evolution. Population dynamics is most deeply rooted in ecology, where biologists and mathematicians have been investigating the dynamics of interacting animal, plant, or microbial species for centuries, via observations, theoretical considerations, and more recently by means of experiments in engineered, controlled environments. However, its principles as well as basic mathematical and computational tools have been successfully applied to an extremely diverse range of fields, such as the study of bio-chemical reactions, genetics, laser physics, economics, epidemiology, and the analysis of cancerous growths, to list but a few. It has hence become a foundational subfield of non-equilibrium statistical physics. In this review, we chiefly focus our attention on the population dynamics of spatially extended Lotka-Volterra predator-prey models.

I. INTRODUCTION

While non-spatial and well-mixed systems already exhibit intriguing properties, the explicit inclusion of spatial degrees of freedom that allow the propagation and mutual invasion of species may lead to the appearance of fascinating spatio-temporal patterns that include activity fronts, traveling waves, and spiral structures characteristic of excitable media. While the deterministic nature of mean-field equations, with the possible extension to spatially extended systems via the inclusion of, e.g., diffusive spreading, already yields important insights into the dynamics of competing populations, the explicit incorporation of stochasticity can fundamentally change and renormalize the behavior of a system of interacting species. In this project we focus our attention on the Lotka-Volterra (LV) model, the most common predator-prey model, and how it behaves when spatial degrees of freedom and stochasticity are implemented.

Volterra argued that the growth rate of the prey population density b, given as $b^{-1}db/dt$, should be a decreasing function of the predator density a and greater than zero when the predator density is zero. Conversely, the predator growth rate $a^{-1}da/dt$ should increase with the prey count, but be negative when $b = 0$. The simplest coupled set of non-linear differential equations following these arguments represents the LV competition model that describes the population densities of predators a and prey b:

$$\frac{da(t)}{dt} = a(t)[\lambda b(t) - \mu], \frac{db(t)}{dt} = b(t)[\sigma - \lambda a(t)] \qquad (1)$$

where t denotes the continuous time. The parameters λ, μ, and σ describe the phenomenological predation, predator death, and prey reproduction rates, respectively. This set of coupled ordinary differential equations gives rise to characteristic, undamped, non-linear oscillations, see $Figure$ 1.

II. SPATIO-TEMPORAL LV MODELS

One may view these coupled ordinary non-linear differential equations (1) as the well-mixed, deterministic limit for time evolution of the mean populations of a system of two interacting predator and prey species. The microscopic and more general LV reaction rules from which equations derive are given by:

$$B \xrightarrow{\sigma} B + B, \quad A \xrightarrow{\mu} \emptyset, \quad A + B \xrightarrow{\lambda} A + A \qquad (2)$$

The prey B reproduce with rate $\sigma > 0$; the predators A spontaneously die with rate $\mu > 0$; and upon encountering each other in their immediate vicinity, both species may interact with (microscopic) predation rate $\lambda > 0$, whereupon the participating prey is consumed while the predator generates one offspring.

If implemented on a lattice, one may in addition allow for nearest-neighbor (or more long-range) particle hopping processes with rate D, associated to continuum diffusivity; alternatively, random particle exchange can be implemented. If one imposes the restriction that each lattice site can at most be occupied by a single individual, prey birth entails that the offspring particle be placed on an adjacent position; likewise, the predation reaction

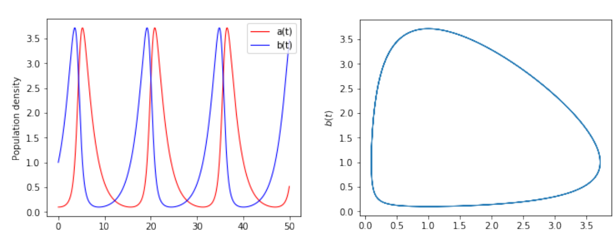

FIG. 1. Left: Characteristic non-linear LV mean-field oscillations of predator (red) and prey (blue) populations over time obtained through numerical integration of the rate equations with parameters $\sigma = \mu = \lambda = 0.5$ and initial densities $a(0) = 0.1$, $b(0) = 1$. Right: The oscillatory dynamics implies closed orbits (neutral cycles) in population density phase space.

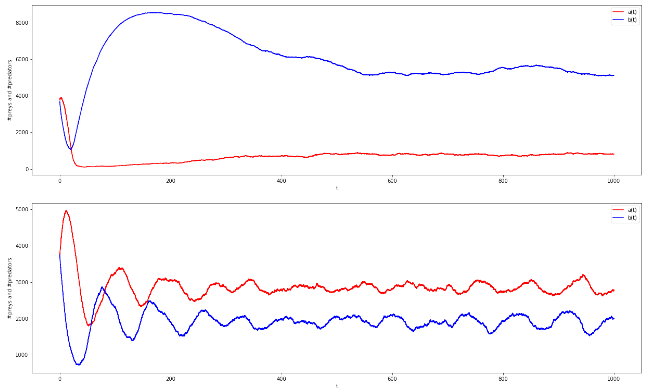

FIG. 2. Early time evolution for the population density of predators $a(t)$ (red) and prey $b(t)$ (blue) in a stochastic two-dimensional lattice LV model with 100 x 100 sites (periodic boundary conditions, and one occupation number restriction) from two single runs that both started with equal particle distribution $a(0) = 0.5$, $b(0) = 0.5$, and with reaction rates (Up) $\sigma = 0.1$, $\mu = 0.2$, $D = 1$ and $\lambda = 1$, and (Down) $\sigma = 0.4$, $\mu = 0.1$, $D = 1$ and $\lambda = 1$.

must then involve two neighboring lattice sites. These processes then automatically generate diffusive population spreading. Note that these coupled rate equations (1) entail a mass action factorization of a two-point correlation function that encodes the likelihood of predators and prey meeting each other at given location at the same time into a simple product of their average uniform densities a and b; hence spatio-temporal correlations are manifestly ignored in this approximate and, in general, rather crude description.

III. IMPLEMENTATION

The stochastic LV model (2) can be implemented on a d-dimensional lattice, usually with periodic boundary conditions to minimize edge effects, in a straightforward manner via individual-based Monte Carlo update rules. One may either allow arbitrarily many predator or prey particles per site, or restrict the site occupancy representing a finite local carrying capacity. For example, one detailed Monte Carlo algorithm on a two-dimensional square lattice with site restrictions (at most a single particle allowed per site) proceeds as follows:

- Select a lattice occupant at random and generate a random number r uniformly distributed in the range $[0, 1]$ to perform either of the following four possible reactions (with probabilities D, σ, μ, and λ in the range $[0, 1]$):
- If $r < 1/4$, select one of the four sites adjacent to this occupant, and move the occupant there with probability D, provided the selected neighboring site is empty (nearest-neighbor hopping).
- If $1/4 \leq r < 1/2$ and if the occupant is an A particle, then with probability μ the site will become empty (predator death, $A \to \emptyset$).
- If $1/2 \leq r < 3/4$ and if the occupant is an A particle, choose a neighboring site at random; if that selected neighboring site holds a B particle, then with probability λ it becomes replaced with an A particle (predation reaction, $A + B \to A + A$).
- If $3/4 \leq r < 1$ and if the occupant is a B particle, randomly select a neighboring site; if that site is empty, then with probability σ place a new B particle on this neighboring site (prey offspring production, $B \to B + B$).

One Monte Carlo step is considered completed when on average each particle present in the system has been picked once for the above processes. If arbitrarily many individuals of either species are allowed on each lattice site, all reactions can be performed locally, but then hopping processe need to be implemented explicitly to allow diffusive propagation.

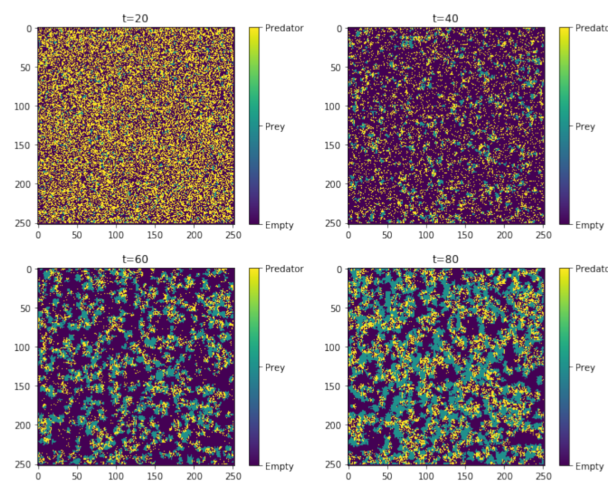

FIG. 3. Snapshots from a two-dimensional stochastic lattice LV simulation with 250 x 250 sites (periodic boundary conditions, one particle per site restriction), $a(0) = 0.7$, $b(0) = 0.3$, $\sigma = 0.5$, $\mu = 0.1$, $D = 0$ and $\lambda = 1$. Here, the prey community survives an early predator invasion, followed by prey recovery and proliferation due to predator scarcity.